

NEW EVIDENCE OF A SPIRIFERIDE ANCESTOR FOR THE THECIDEIDINA (BRACHIOPODA)

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ABSTRACT. Investigation of the microstructure of the ventral interarea of a juvenile denticulate spiriferacean assignable to *Unispirifer* reveals rod-like structures which, apart from a difference in size, are structurally almost identical with the tubercle cores of a recently discovered Aalenian thecideidine species *Mimikonstantia sculpta* Baker and Elston, 1984. The coincidence of cyrtomatodont teeth, shell resorption, and secondary fibrous shell, together with rod-like granular calcite structures ensheathed in secondary fibres, links the thecideidines with denticulate spiriferaceans. Comparison of the thecideidine shell microstructure with that of a stropheodontid strophomenide *Amphistrophia* has failed to reveal comparable microstructural elements. The new evidence indicates that the spiriferacean denticle is a structural homologue of the thecideidine tubercle and, from a systematic point of view, removes any remaining objection to the formal assignment of the Thecideidina as a suborder of the Spiriferida. The morphological similarity between thecideidines, suessiacean spiriferides, and certain davidsoniacean and productidine strophomenides is now regarded as an expression of homoeomorphy.

IN recent years attention has centred on the question of whether the thecideidine brachiopods share affinity with the Strophomenida or the Spiriferida. The main arguments in favour of derivation from strophomenide stock were advanced by Rudwick (1968) and Baker (1970) who supported the idea of descent from the Davidsoniacea. Pajaud (1970) and Grant (1972) similarly argued for a strophomenide ancestor but were in favour of derivation from productidine stock. The only strong dissent was voiced by Williams (1968, 1973) who, on the basis of shell microstructure, suggested that the thecideidines were derived from spiriferide stock and, more specifically, from the Suessiacea. The importance of neoteny in thecideidine evolution has been repeatedly stressed (Elliott 1953; Pajaud 1970; Williams 1973). If neoteny has exerted the profound influence which most workers believe to be true, the early thecideidines are likely to bear a much closer resemblance to juveniles of ancestral forms than to their adult counterparts. Unfortunately, early juveniles are not only less common than adults of the species but also more difficult to identify. After reviewing the morphological and microstructural evidence, Williams (1973, p. 466) concluded that certain persistent characters in the various thecideidine lineages were of fundamental phylogenetic significance. He identified shell microstructure as probably the most important character. The question posed, therefore, is whether the shell microstructure of early middle Jurassic thecideidines represents an ontogenetic ancestral character which through neoteny became 'frozen' into an adult shell fabric.

Work in progress on the preservation of ontogenetic relics in the shell fabrics of adult articulate brachiopods pinpoints the umbonal region of the brachial valve and, where no shell resorption has occurred, the pedicle valve also, as an area of great importance in the determination of phylogeny. However, because of the effects of neoteny, the solution to the problem of thecideidine affinity may never be reached through study of adult shell fabrics of even immediate potential ancestors. The aim of the current investigation has been, therefore, to establish whether the shell fabrics of juvenile representatives of Palaeozoic spiriferide and strophomenide genera provide unequivocal evidence of spiriferide or strophomenide affinity. Unfortunately, within the Thecideidina the shell microstructure exhibits such a bewildering variety of detail that it becomes difficult to isolate those characters which are of major significance. However, in spite of the drastic changes which affected the shell microstructure of the later representatives of the group, studies have shown that tubercles and secondary fibrous shell are characteristic and persistent features of the thecideidine shell (Baker 1970; Baker and Laurie 1978; Smirnova 1979; Williams 1973). When traced back to early representatives of the group, the tubercles are found to originate as cored structures in forms with a normal (*sensu*

Williams 1968) secondary fibrous layer. Since tubercle cores seem to be a fundamental feature of the thecideidine shell structure, persisting throughout the history of the group, it seems reasonable to assume that similar structures would be a character of the ancestral stock. The shell microstructure of juveniles of certain spiriferide and strophomenide genera was investigated with this in mind.

Registration of material. The material investigated in this study is to be housed in the British Museum (Natural History) as BB81115–81119. The BM(NH) specimens referred to in the discussion are relocated as numbers BB84702 (complete shell *ex* tubed specimens B32375D) and BB84703 (pedicle valve *ex* tubed specimens B32376B).

Preparation of material. Sufficiently large specimens were cut at the required orientation using a Logitech 'Trimsaw'. The cut face was then finished, using F800 C6 black silicon carbide abrasive powder, followed by etching for ten seconds in 5% hydrochloric acid. Small specimens were mounted in cold-setting resin before being subjected to the above preparation technique. All material selected for stereoscan electron microscopy was gold-coated before photography.

SHELL MICROSTRUCTURE

Spiriferide shell microstructure. The shell microstructure of spiriferide brachiopods has been the subject of a detailed study by MacKinnon (1974) and it is not necessary to add to his account of the general shell fabric encountered. He appears, however, to have overlooked aspects of the shell microstructure of denticulate spiriferaceans such as *Unispirifer*. This is unfortunate as investigation of the umbonal region of juveniles of lower Carboniferous specimens has provided the first clear evidence of structures in spiriferides which, apart from differences in size and orientation relative to the external surface of the shell, are otherwise identical with the tubercles found in the pedicle valve of certain basal middle Jurassic thecideidines.

The general shell microstructure of *Unispirifer* is identical with that of other spiriferacean genera studied by MacKinnon (1974). Study of the surface of the ventral interarea of well-preserved juveniles, however, reveals the presence of a parallel series of granular calcite-filled grooves aligned perpendicular to the hinge line (Pl. 77, fig. 1). Unfortunately, the umbonal regions of all the available specimens have suffered some abrasion or exfoliation so that the primary shell is nowhere complete. The best-preserved material, however, clearly shows that on the ventral interarea the striae, orientated at right angles to the hinge axis, are really in-sunk areas of primary shell which become more pronounced as the primary layer is lost (Pl. 77, fig. 2). Sections parallel with the hinge axis and perpendicular to the surface of the interarea show that the grooved areas are underlain by trough-like invaginations around which the secondary shell mosaic is deflected (Pl. 77, figs. 3, 4), indicating that the intervening ridges are an artefact produced by removal of shell material from the grooves.

EXPLANATION OF PLATE 77

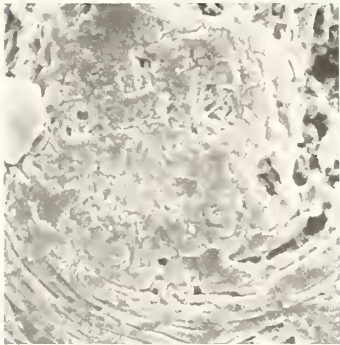
Figs. 1–8. *Unispirifer* sp., juvenile specimens, north Derbyshire (precise horizon and locality unknown), Viséan limestones, lower Carboniferous. BB81117 (figs. 1–5), BB81118 (fig. 8), and BB81119 (figs. 6, 7). 1, oblique view of ventral interarea, hinge-line upper right, showing the ridges and grooves formed by removal of the majority of the primary shell layer, $\times 45$. 2, surface view showing the granular calcite-filled troughs which deflect the secondary shell fibres, $\times 80$. 3, transverse section, parallel with hinge axis, through ventral interarea to show detail of the way in which the granular calcite filling a trough deflects the secondary shell fibres, $\times 400$. 4, exfoliated region, same orientation as fig. 3, showing detail of a trough from which the granular calcite has been removed, $\times 250$. 5, oblique view, ground surface top right, to show the rod-like (accentuated by etching) nature of the granular calcite body occupying the trough, $\times 250$. 6, section parallel with surface of ventral interarea showing the granular calcite, together with traces of a gross pseudo-fibrous mosaic, of a denticle and its associated core in longitudinal section, $\times 400$. 7, detail of the granular calcite of the denticle core in fig. 6, location as indicated, $\times 3000$. 8, surface view of ventral interarea showing detail of primary layer (left) overlying a denticle core, and the fibrous secondary shell (right) adjacent to it, $\times 800$. Stereoscan photomicrographs.



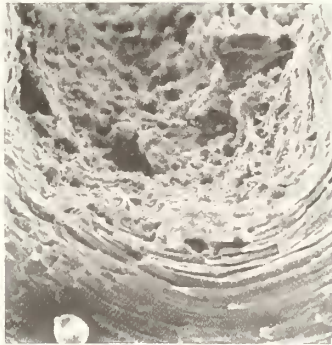
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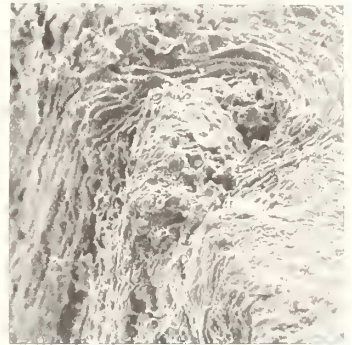
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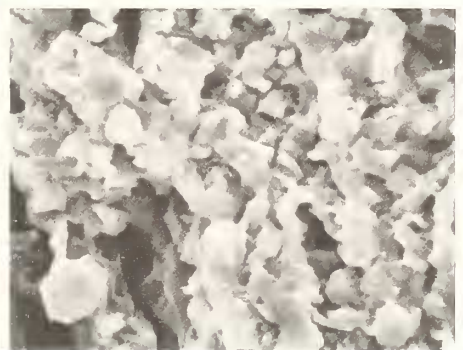
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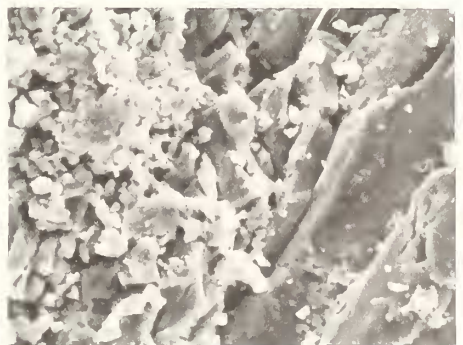
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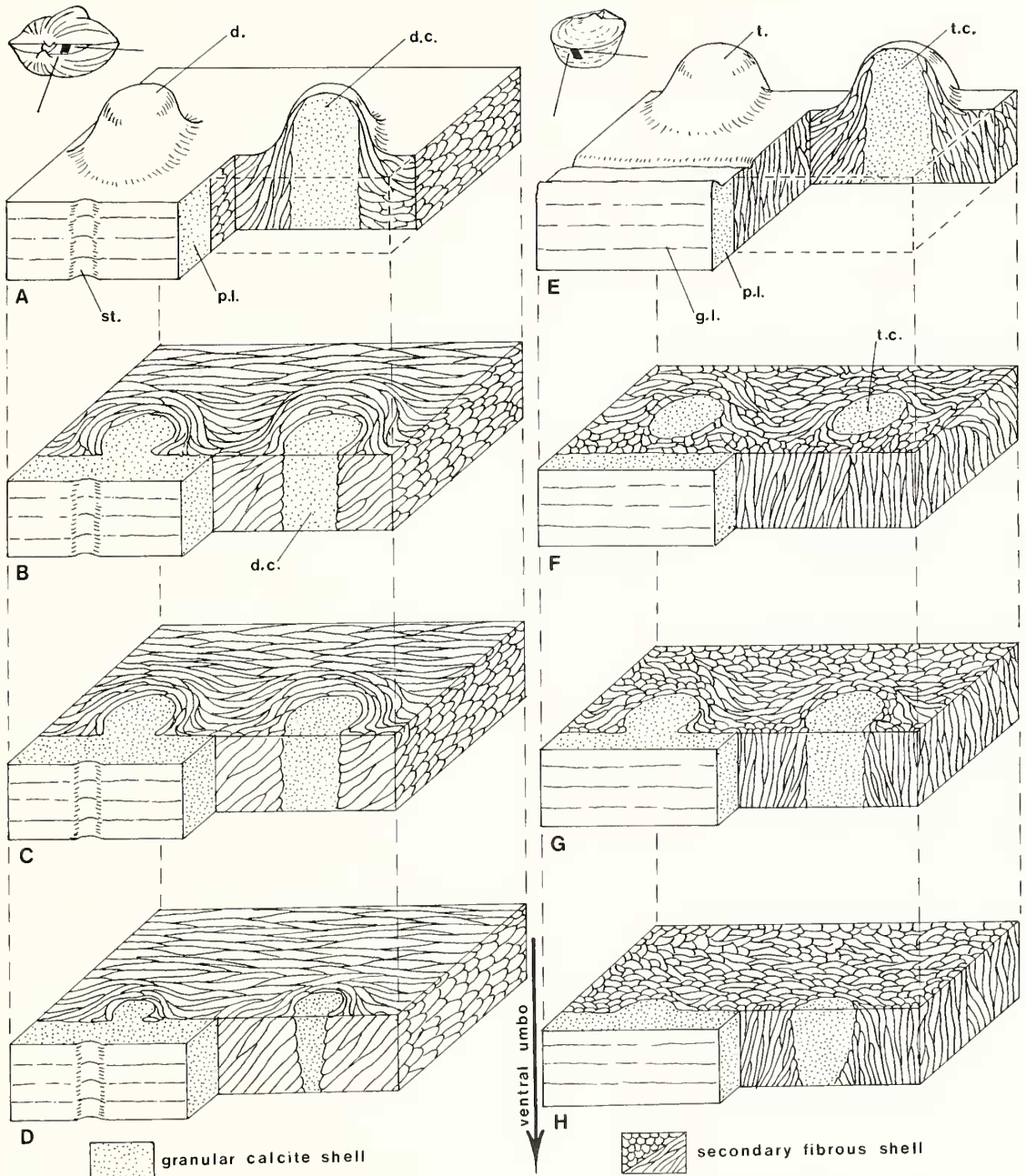
Specimens in which the structures are partially exfoliated (Pl. 77, fig. 5), and sections parallel with the surface of the interarea (Pl. 77, fig. 6), show that the troughs are occupied by rod-like bodies of granular calcite approximately 80 μm in diameter, whose outer surface remains in contact with the primary layer along their length (text-fig. 1B-D). Longitudinal sections through the rod-like bodies (Pl. 77, fig. 6) show them to be continuous with the denticles developed along the hinge margin. Although the shell material of the denticle core is clearly granular calcite (Pl. 77, figs. 7, 8), a gross fibrous mosaic appears to be discernible (Pl. 77, fig. 6) and is discussed later. The in-sunk condition of the denticle cores of *Unispirifer* is apparently different from that of the upper Devonian *Tenticospirifer* whose denticles were depicted by Williams and Rowell (1965, p. H94, fig. 100C, E) as forming denticular ridges on the surface of the interarea.

Thecideidine shell microstructure. The presence of cored tubercles in both valves of the shell of *Moorellina granulosa* (Moore) has been demonstrated by Baker (1970). The tubercles of the brachial valve were shown to have granular cores aligned almost perpendicular to the primary shell layer, whilst those of the pedicle valve had cores of conically arranged fibres aligned almost parallel with the inner surface of the primary layer (Baker 1970, p. 91, text-fig. 6). Williams (1973), in his detailed and comprehensive study of Recent and the majority of fossil thecideidine taxa, demonstrated that the evolution of the group was characterized by the neotenus suppression of the fibrous secondary layer; he identified the main onset of the sporadic secretion of secondary shell as a late Jurassic or early Cretaceous event. The recent discovery of a new genus (Baker and Elston 1984) clearly shows that in one stock at least the suppression of secondary shell was well advanced by basal middle Jurassic times. *Mimikonstantia sculpta* possesses cored tubercles and those of the brachial valve have granular calcite cores (Baker and Elston 1984, pl. 71, fig. 2) almost identical with those found in *Moorellina granulosa*. The tubercles of the pedicle valve of *Mimikonstantia sculpta*, however, have attenuated granular calcite cores (Baker and Elston 1984, pl. 71, figs. 6, 7) approximately 40 μm in diameter, in sharp contrast with the fibrous cores of *Moorellina granulosa* although their orientation approximates even more closely to an alignment parallel with the primary layer (text-fig. 1F-H). A significant difference between the shell fabric of *M. granulosa* and *Mimikonstantia sculpta* is that in the latter species the secondary fibrous shell layer is greatly reduced in thickness and is underlain by granular calcite. In this respect the shell of *M. sculpta* very closely resembles that of Cretaceous genera such as *Thecidiopsis*.

Strophomenide shell microstructure. Laminar shell (Williams 1968) is, with few exceptions (Williams 1970), a fundamental character of the strophomenide shell although, as Williams concluded (1970, p. 339), the strophomenides must have evolved from fibrous-shelled ancestors. It was important therefore, because of the possibility of a pedomorphic origin of the thecideidine shell fabric, to examine the shell microstructure of certain juvenile strophomenides to try to ascertain whether any of the characters could be correlated with those observed in the thecideidine shell. The discovery of the granular calcite core in the denticles of the spiriferacean ventral interarea necessitated an investigation of the interareas of stropheodontid strophomenaceans, in order to establish whether the microstructure of the stropheodontid denticle exhibited characters correlateable with the thecideidine tubercle. Horizontal and transverse sections through the ventral interarea of an upper Silurian juvenile *Amphistrophia* show that the denticles are cored structures (Pl. 78, figs. 1, 2). Like pseudopunctae, however, the denticles have a core of crystalline calcite enveloped in typical laminar shell in which the laminae are deflected distally (Pl. 78, figs. 3-5). The denticles, therefore, appear to originate in the same way as pseudopunctae and, in view of the distribution of the occurrence of pseudopunctae throughout the Strophomenida, may be regarded as modified pseudopunctae.

DISCUSSION

If the thecideidines arose neotenusly (Elliott 1953; Pajaud 1970; Williams 1973) or pedomorphically (Williams and Rowell 1965), the validity of conclusions drawn from comparison of morphological



TEXT-FIG. 1. Exploded block reconstructions (not to scale). A-D, *Unispirifer*, small section of the ventral interarea (location as indicated) of a juvenile to show the relationship between the primary shell layer and the denticle cores. E-H, *Mimikonstantia*, small section of the free ventral wall (location as indicated) of the pedicle valve to show the relationship between two comparable tubercle cores and the primary shell layer. d., denticle; d.c., denticle core; g.l., growth line; p.l., primary shell layer; st., striation; t., tubercle; t.c., tubercle core.

characters may be considerably weakened. There is also an explanation other than genetic relationship for the morphological similarity between thecideidines, davidsoniacean strophomenides, and suessiacean spiriferides. Work by Cooper and Grant (1974) on the beautifully preserved reef-associated Permian faunas of West Texas showed that many of the Permian forms which most closely resemble thecideidines were an abundant element of patch reef faunas. Other studies (Baker 1981, 1983) established that middle Jurassic thecideidines were characteristically associated with patch reefs or coralliferous debris adjacent to patch reefs. Among the brachiopods there is a clear correlation between typically conical pedicle valves, loss of pedicle, complete delthyrial covers, weakly convex brachial valves, and the association with reefs. In short, the characters may be regarded as a response to environmental pressure, a view which is confirmed by the characteristic morphology of richthofenid brachiopods and rudistid bivalves. Williams (1973) drew attention to the danger of ascribing genetic significance to characters of convergent origin. It now seems probable that the morphological similarity between davidsoniaceans, suessiaceans, and thecideidines is environmentally induced; in which case, the davidsoniacean and suessiacean genera previously regarded as genetic relatives of the thecideidines are nothing more than heterochronous homoeomorphs. Therefore, in attempting to trace affinity, attention must be focused on characters which are likely to be less susceptible to environmental pressure.

Although morphological comparison is suspect, there are certain characters which appear to be so fundamental to thecideidines and their ancestral stock that none of the caenogenetic changes contributing to the emergence of the thecideidines (Williams 1973, p. 469) was sufficiently profound to be able to mask them. Jaanusson (1971) noted that brachiopod teeth were either deltidodont or cyrtomatodont, and that with only two exceptions forms with deltidodont teeth did not acquire the ability to use resorption for the construction of their shells. This frequently overlooked observation has profound implications for any proposed strophomenide (deltidodont) line of descent because the ability to resorb shell material is of such crucial importance for the construction of thecideidine (cyrtomatodont) shells that it is almost certain to be a capability shared by their immediate ancestors. Similarly, tubercles are such a persistent feature of the thecideidine shell that they should, together with fibrous secondary shell, be traceable back to the ancestral stock.

Baker (1970) concluded that a better knowledge of the Triassic genus *Thecospira* was critical to an understanding of thecideidine systematics. Three significant contributions (Dagis 1973; Williams 1973; MacKinnon 1974) were soon forthcoming and it is perhaps unfortunate that they served only to polarize still further the views already held. Dagis (1973) supported the views of Rudwick (1968,

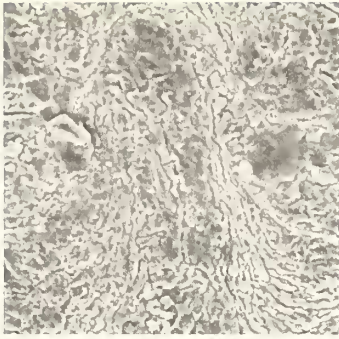
EXPLANATION OF PLATE 78

Figs. 1-5. *Amphistrophia funiculata* (M'Coy), juvenile specimens, Wren's Nest, Dudley, Much Wenlock Limestone Formation, upper Silurian. BB81115 (figs. 1, 4, 5), BB81116 (figs. 2, 3). 1, transverse section through hinge area showing crystalline calcite denticle core in longitudinal section, flanked by laminar shell, $\times 400$. 2, horizontal section through hinge area showing crystalline calcite denticle core in transverse section, flanked by laminar shell, $\times 1000$. 3, horizontal section through lateral region showing crystalline calcite taleola in transverse section, flanked by laminar shell, $\times 1000$. 4, transverse section through the shell showing laminar shell deflected by a taleola, $\times 400$. 5, detail of laminar shell in transverse section, $\times 1000$.

Figs. 6-8. Aff. *Moorellina*. BB84702, Dundry Hill, Bristol, Inferior Oolite (precise horizon and locality unknown). 6, brachial view, showing striations on ventral interarea, $\times 15$. 7, angled view (tilt angle 25°) of ventral interarea with ridge and groove structure perpendicular to hinge axis, $\times 35$. 8, part of ventral interarea showing detail of ridge and groove structure, and granular nature of the shell, $\times 400$.

Figs. 9-12. Cf. *Moorellina*. BB84703, Dundry Hill, Bristol, Inferior Oolite (precise horizon and locality unknown). 9, angled view (backward rotation 50°) showing row of small tubercles along hinge-line, $\times 12$. 10, part of hinge-line showing tubercles in more detail, $\times 100$. 11, broken hinge tubercle showing its apparently granular structure, $\times 1000$. 12, surface view of part of hinge tooth showing clearly defined fibrous structure, for comparison with hinge tubercle in fig. 11, $\times 1500$.

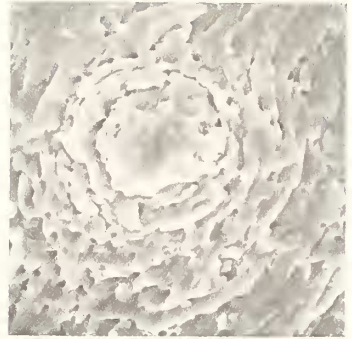
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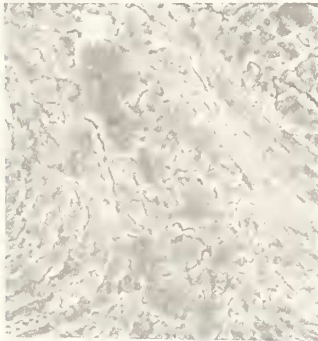
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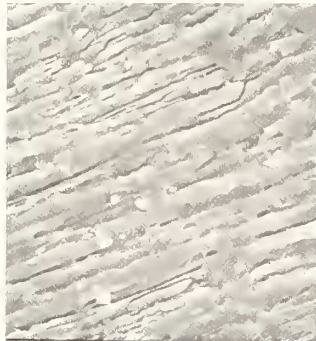
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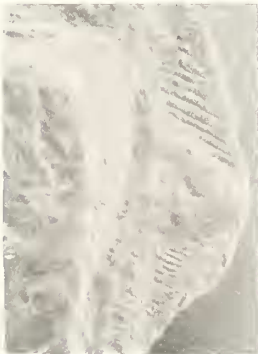
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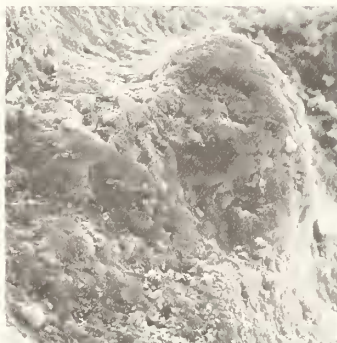
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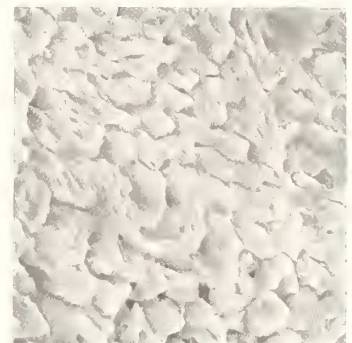
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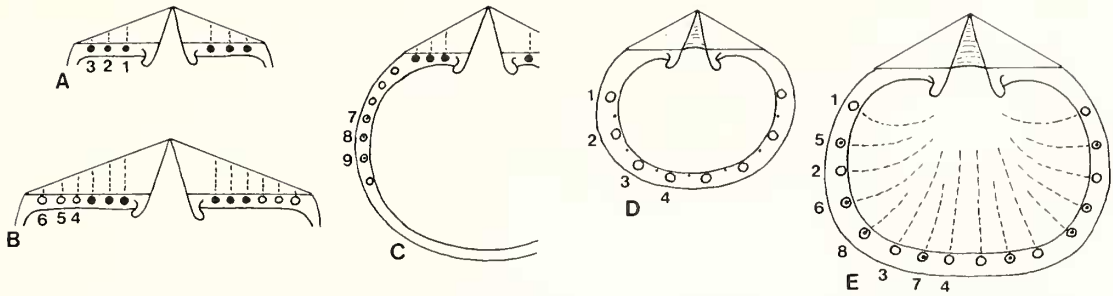
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1970) and Baker (1970) that *Thecospira* was of strophomenide affinity. Williams (1973), however, reiterated his earlier (1968) view that *Thecospira* was of spiriferide affinity. Williams's view was supported by MacKinnon (1974) in his comprehensive survey of spiriferide shell structure which included a detailed study of the microstructure of *Thecospira* from the Triassic St. Cassian Beds of northern Italy. Dągis (1973) studied a wider range of material than was available to MacKinnon and established beyond doubt that the shell structure of thecospirids is almost identical with that of middle Jurassic thecideaceans, such as *Moorellina* and *Minikonstantia*, even to the extent of the dissimilarity of the structure of the brachial and pedicle valves. Thecospirids, therefore, both morphologically and in the organization of their secondary shell fabric, are much closer to thecideidines than they are to any undoubted spiriferides and there can be little doubt that the relationship is a genetic one. Dągis (1973, p. 367) concluded that among the thecospirids *Hungaritheca* is in all probability ancestral to the Thecideidina. I agree that *Hungaritheca*, if not actually ancestral to the thecideidines, is certainly very close to the thecideidine line of descent. The plexus of descent of the thecideidines is thus inextricably linked with the derivation of the thecospirids also. Prior to Dągis's (1973) evidence, I had previously expressed the opinion that thecideidine tubercles might be the functionally modified homologue of the strophomenide pseudopunctae (Baker 1970, p. 97). This opinion must now be revised as granular calcite appears to be the primitive tubercle core material in thecideidines. The evidence is also weak from a pedomorphic point of view as the strophomenide taleola, even at a very early age, is characteristically flanked by laminar shell (Pl. 78, fig. 5). It now seems, therefore, that the strophomenide pseudopunctae have no counterpart among the Thecideidina. Consequently, the contention that the thecideidines might be descended from strophomenide ancestors is not supported by the present study.

In view of the demonstrable link between thecideidines and thecospirids, an important consideration arising from the new evidence is whether a similar link exists between the thecideidines and the spiriferaceans. In both *Unispirifer* and *Mimikonstantia* the rod-like granular calcite bodies possessed a distal accretion zone that remained slightly in advance of the secretion of secondary fibres which were subsequently deflected. Their growth pattern caused them to emerge along the hinge line as a row of tiny denticles in *Unispirifer* (text-fig. 1A) and along the inner margin of the valve edge as a row of small tubercles in the pedicle valve of *Mimikonstantia* (text-fig. 1E). In *Unispirifer* the denticle cores maintain a connection with the primary layer throughout their length (text-fig. 1B-D). Such cores would most easily have been formed by an invagination of the primary layer which, in the case of *Mimikonstantia*, may be regarded as having become 'pinched off' from the primary layer during their development (text-fig. 1F, G) to become totally ensheathed in secondary fibres. In *Unispirifer* the orientation of the denticles must mean that they were generated consecutively (text-fig. 2A, B) as the hinge line increased in length. Once initiated, the structures apparently continued to develop during the life of the animal. In *Mimikonstantia* on the other hand the tubercles show a systematic intercalary generation pattern (text-fig. 2D, E) which may be reconciled with the need to ensure the effective maintenance of the continuity of arrangement and location of the tubercles along the inner margin of the pedicle valve as growth proceeded. The difference in the location of the structures in the two genera is not a serious problem. Both sets of structures are sequential, with early and later representatives, and the arrangement of the tubercles bears the same relationship with the ventral umbo (text-fig. 1) irrespective of whether the structures are located in the ventral interarea or in the wall of the ventral valve. All that is required is a slight change in the growth pattern of the shell. Thecideidines have a relatively much shorter hinge line than spiriferaceans; therefore, if the trend towards the shortening of the hinge line was independent of the tubercle generation pattern, a slight change in the growth pattern of the shell could have resulted in the development of the structures along the lateral (text-fig. 2C) and, ultimately, the anterior margin of the valve. The same development pattern may have been triggered by a slight change in functional requirements (e.g. reef-association), in which case the change to an intercalary development pattern and the elimination of denticles and the appearance of tubercles in thecideidines may be explained as an evolutionary development.



TEXT-FIG. 2. Generalized diagrams to compare consecutive development patterns. A, B, *Unispirifer*, denticles in the ventral interarea as the hinge-line increases in length. D, E, *Mimikonstantia*, essentially intercalary pattern of the tubercles round the anterior border of the pedicle valve as the shell increases in size. C, cf. specimen BB84703 (Pl. 78, figs. 9, 10) hypothetical transitional stage with denticles along the hinge-line and tubercles on the lateral margins of the valve.

The above argument would obviously be strengthened if any early thecideidines showing some of the juvenile *Unispirifer* characters could be located. A search of the British Museum (Natural History) collections has revealed two specimens from the Inferior Oolite (horizon uncertain) of Dundry Hill near Bristol. BB84702 is a complete shell, 3.3 mm in width and assignable to aff. *Moorellina*, which has a ventral interarea (Pl. 78, figs. 6–8) showing clearly developed striations perpendicular to the hinge axis. BB84703 is a pedicle valve, 4 mm in width and assignable to cf. *Moorellina*, with a row of tubercles (denticles?) along the hinge line (Pl. 78, figs. 9, 10) in a position similar to that occupied by the denticles of *Unispirifer*. A broken tubercle (Pl. 78, fig. 11) appears to be composed of granular material, whereas the hinge tooth (Pl. 78, fig. 12) clearly displays a fibrous structure. This evidence, considered in conjunction with the microstructure described, convinces me that the spiriferacean denticle is homologous with the thecideidine tubercle. With regard to the thecospirids, Dagis (1973) described a pseudo-fibrous texture for the tubercle cores of the pedicle valve of *Thecospira communis* in which the individual fibres were composed of acicular grains of calcite. Williams (1973) described a similar arrangement in the secondary fibres of the teeth of *Thecidellina barretti* (Davidson). It is interesting that the granular denticle cores of the *Unispirifer* studied here have the appearance of a gross pseudo-fibrous fabric (Pl. 77, fig. 6) which may be correlated with the thecospiriid tubercle cores described by Dagis. Nalivkin (1976, p. 70) noted the presence of low narrow ridges and striae on the interareas of a number of spiriferides and concluded that during life the structures were associated with a covering of byssal attachment filaments. None of Nalivkin's material is available for study but the evidence from the British lower Carboniferous material, which enables the external ridges and grooves to be correlated with underlying structural elements of the interarea, is incompatible with his (1976) interpretation.

CONCLUSIONS

Characteristic though all the features evaluated by Williams (1973) are, the evidence indicates that cyrtomatodont teeth, secondary fibrous shell, tubercles, and the ability to resorb large tracts of shell material must be regarded as criteria of paramount importance in the indication of thecideidine ancestry. The morphological similarity previously cited as evidence of strophomenide or spiriferide affinity may simply reflect homoeomorphy. Shell microstructure, however, demonstrates unequivocally that the thecideidines are genetically related to the thecospirids and it is here recommended that the thecospirids should be assigned, as a taxon of superfamily rank, to the Thecideidina. The establishment of a genetic link between the shell microstructure of early middle Jurassic thecideidine and lower Carboniferous spiriferacean brachiopods leads to the conclusion that, however unlikely it may seem on morphological grounds, spiriferacean forms probably include the ancestral stock from

which the thecideidines and the thecospirids were derived. In this respect it is noted that the upper Devonian *Tenticospirifer* with its hemipyramidal pedicle valve and relatively flattened brachial valve is beginning already to approximate to thecideidine external morphology.

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